

Research review

Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests

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Summary

A growing body of empirical work suggests that soil organisms can exert a strong role in plant community dynamics and may contribute to the coexistence of plant species. Some of this evidence comes from examining the feedback on plant growth through changes in the composition of the soil community. Host specific changes in soil community composition can generate feedback on plant growth and this feedback can be positive or negative. Previous work has demonstrated that negative soil community feedback can contribute to the coexistence of equivalent competitors. In this paper, I show that negative soil community feedback can also contribute to the coexistence of strong competitors, maintaining plant species that would not coexist in the absence of soil community dynamics. I review the evidence for soil community feedback and find accumulating evidence that soil community feedback can be common, strongly negative, and generated by a variety of complementary soil microbial mechanisms, including host-specific changes in the composition of the rhizosphere bacteria, nematodes, pathogenic fungi, and mycorrhizal fungi. Finally, I suggest topics needing further examination.

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Introduction

A wide range of biotic and abiotic factors have been shown to impact the structure and dynamics of plant communities. Historically, however, much of the effort to determine factors structuring plant communities has focused on the importance of abiotic factors, particularly light and soil nutrients, in determining the outcome of interspecific competition (Tilman & Pacala, 1993). Yet, the importance of trophic interactions in plant dynamics has long been appreciated. This appreciation has been fueled by clear examples of above-ground herbivory driving changes in plant community

composition (Tansley & Adamson, 1925; Carson & Root, 2000; Howe *et al.*, 2002). There is also accumulating evidence and a growing suspicion that biotic interactions occurring below-ground may play an equally, if not more, significant role in determining the outcome of plant–plant interactions (Fitter, 1977; Allen & Allen, 1990; Hartnett *et al.*, 1993; Van der Heijden *et al.*, 1998; Packer & Clay, 2000).

Evaluation of the importance of below-ground interactions in plant community dynamics, however, has been hampered by the largely undescribed diversity of soil organisms and the technical problems associated with their measurement and

manipulation. The soil community is fantastically complex. Taxonomically, soil organisms include annelids, arthropods, nematodes, protists, fungi, bacteria and archaea. Our understandings of the diversity within any one of these groups is limited, but recent molecular work has given a glimpse of a world that is exceedingly diverse (Vandenkoornhuys *et al.*, 2002). Similarly, the density of these organisms can be very high. Plant roots, then, live and grow in this microbial milieu. Indeed the association of plant roots and soil organisms is far from incidental – the association of plants and mycorrhizal fungi apparently began with, and may have been essential for, the earliest colonization of land (Pirozynski & Malloch, 1975; Redecker *et al.*, 2000). Plants and soil organisms remain profoundly interdependent. Plant carbon, largely through roots, drives the below-ground food web. As such soil organisms generally benefit directly or indirectly from plants. In turn, soil organisms have direct and indirect effects on plant growth that range from strongly positive (e.g. mycorrhizal fungi) to strongly negative (e.g. damping-off pathogens). Therefore, at a basic level we expect the interaction between plants and their associated soil organisms to range from mutually beneficial to pathogenic. Yet, given the high diversity of soil organisms, characterizing the net effect of soil organisms on plant growth is itself a nontrivial task.

Moreover, the net direct effects of soil organisms on plant growth does not adequately describe the impact of soil organisms on plant dynamics. Soil organisms exert differential effects on the growth of individual plant species. For example, plant species vary widely in their response to arbuscular mycorrhizal (AM) fungi (Adjoud *et al.*, 1996; Smith & Read, 1997; Van der Heijden *et al.*, 1998) and other soil taxa such as soil pathogens (Bruehl, 1987; Agrios, 1997). As a result, while a particular soil organism might have positive direct effects on a particular plant species, the net effect might be negative due to larger positive effects on a competing plant species.

Conversely, soil organisms can respond differentially to plant taxa. AM fungi, for example, while associating broadly with plant hosts, have been repeatedly shown to have host-specific growth responses (Bever *et al.*, 1996; Eom *et al.*, 2000; Bever, 2002a). Again, this same pattern holds for rhizosphere bacteria and soil microfungi (Westover *et al.*, 1997; Hadacek & Kraus, 2002). As a result the composition of the soil community will change as a result of association with different plant species. These host-specific changes in the soil community can then feed back directly on the growth of the host plant species. The host-specific changes in the soil community may also alter the growth of competing plant species. The net effect of the soil community composition on plant community dynamics will depend on both the direct feedback on host growth and the indirect effects on competing plant (Bever *et al.*, 1997).

I have previously advocated the utility of a feedback approach to assessing the impact of below-ground interactions

on plant dynamics (Bever, 1994; Bever *et al.*, 1997; Bever *et al.*, 2002). This approach has been found to be useful in investigating the dynamics in several community types (Holah & Alexander, 1999; Olf *et al.*, 2000; Packer & Clay, 2000; Klironomos, 2002). In this paper, I extend the conceptual framework of feedback and then review the evidence for such feedback in plant communities. I finally explore the implications and limitations of our current state of knowledge of soil community feedback.

The basics of soil community feedback on plant growth

The presence of a particular plant will cause a vast suite of changes in the composition of the soil community, as organisms that have high relative growth rates on that species of plant increase. As the composition of the soil community changes due to its host, the net effect of the soil community on the growth of this plant species will also change, causing a feedback between below-ground community composition and plant growth rate. By feedback, then, I mean a two-step process in which the presence of a plant changes the composition of the soil community and then that change in the soil community alters the growth rate of that plant type. The change in the soil community can alter the growth rate of the plant host directly (as represented by parameters α_A and β_B in Fig. 1) or indirectly through changes in the growth of competing plant species (as represented by parameters α_B and β_A in Fig. 1). The effect of the soil community on plant community dynamics depends upon the relative magnitude

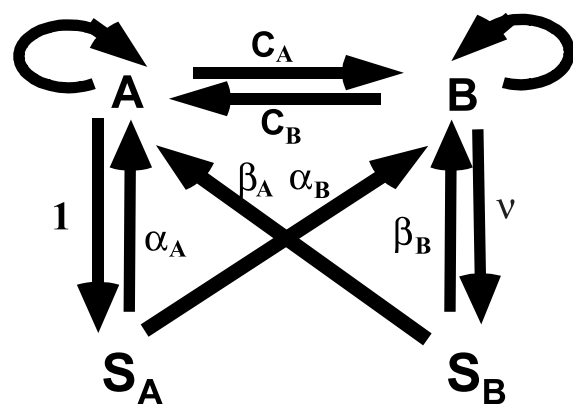


Fig. 1 In this figure, we present the potential interactions between two plant species, A and B, and their soil communities, represented by S_A and S_B , respectively. The presence of plant A causes a change in its associated soil community (i.e. an increase in S_A) that can then directly alter the growth of plant A, represented by the parameters α_A , or alter the growth of plant B, represented by the parameter α_B . Similarly, plant B can have direct feedback on its own growth, represented by β_B , as well as indirect feedback through changes in the growth of plant A, represented by the parameter β_A . The two plant species can also have direct density dependence on their own growth and competitive effects on each other's growth.

of these effects (Bever *et al.*, 1997). If all of the effects were equivalent ($\alpha_A = \alpha_B = \beta_A = \beta_B$), the soil community would not alter the interaction between plant species.

However, interaction strengths will not be homogeneous. Soil community feedback is therefore expected given that soil organisms respond differently to host identity and that individual soil organisms affect plant growth differently. Associations between plants and soil microbes range in their specificity from the highly specific orchids mycorrhizas and the cosmopolitan rhizosphere bacteria. The specificity of association (i.e. the ability to form specific associations) between plants and microbes is distinct from the specificity of the plant and microbe response to their association (i.e. the dependence of relative fitness on specific associations). While these two levels of specificity are not completely independent, they are not necessarily collinear either. Although, interactions that have relatively high specificity of association (e.g. ectomycorrhizas), might be expected to show relatively high specificity of response, those with low specificity of association (e.g. arbuscular mycorrhizas), can also show high specificity of response: the growth of plant species varies with species of AM fungi (Adjoud *et al.*, 1996; Van der Heijden *et al.*, 1998; Helgason *et al.*, 2002) and the growth of species of AM fungi also depends on the identity of the plant with which they are associated (Bever *et al.*, 1996; Eom *et al.*, 2000; Bever, 2002a). In fact, soil microbes commonly show specificity of response to plant species and specificity of growth effects on those hosts, although this is rarely measured. This level of specificity within the soil community will generate feedback on host growth (Bever, 1999).

Theory of soil community feedback

Given the profound diversity of organisms in the soil, a complete description of the impact of a plant species on the composition of the soil community would be a formidable, if not impossible task. Yet, one might comfortably suggest that the continued association with a single plant species would drive the composition of the soil community toward a dominance of those types that have highest growth rates on that plant type. Alternatively, continued association with a second plant species might drive the composition of the soil community in a separate direction. The composition of the soil community present at any one time might then be usefully scored according to its relative position between these two endpoints. Effectively, we are projecting the position of the multidimensional soil community onto a single axis that describes the relative influence of the two plant types. Formally, the soil community can be scored according to the relative influence of plant A, S_A (Fig. 1). When the soil community is dominated by organisms with high relative growth rates on plant A, S_A will approach one. S_A approaches zero when the soil community is dominated by organisms with high relative growth rates on plant B. The parameters α_A ,

α_B , β_A , and β_B describe the effects of these changes in soil community composition on growth of the two plant species (Fig. 1).

Clearly there are many limitations imposed by reducing the dimensionality of the soil community to a single axis. Soil organisms might differ in their rates of host-specific changes and as these organisms may vary in their effects on host growth, this could cause nonlinearities of the feedback terms. Nonlinearities in feedback may also result from changes in the soil community that result from trophic interactions within the soil community. Such effects have been shown to be important in agricultural settings (Larkin *et al.*, 1993). The host-specific endpoints (and therefore the soil community feedback) will also depend upon the initial composition of the soil community.

The great advantage of reducing the dimensionality of the soil community as in Fig. 1 is that it allows us to begin to analyze the impact of soil community dynamics on plant community processes. When the effects of soil community changes are plant species dependent (i.e. α_A , α_B , β_A , and β_B are not equal), then there will be feedback on plant growth. To describe the impact of the soil community feedback on the dynamics of plant populations and communities, I analyze the model depicted in Fig. 1 more formally. A complete description of the dynamics of two plant species and their effects on the soil community would require four interdependent differential equations – a level of complexity beyond what one can easily analyze. I had previously reduced the system to two equations by assuming that the plant species were equivalent competitors and avoiding explicit consideration of density dependence (Bever *et al.*, 1997). Here, I summarize these results and then extend this model by investigating the joint effects of soil community feedback and interspecific competition (Fig. 1).

The influence of the soil community feedback on plant species coexistence

Reducing the overall complexity by assuming that the plant species were equivalent competitors and avoiding explicit consideration of density dependence, I found that the net dynamics depend upon the sign of an interaction coefficient, I_s , where $I_s = \alpha_A - \alpha_B - \beta_A + \beta_B$ (Bever *et al.*, 1997). When the interaction coefficient is positive ($I_s > 0$), the soil community dynamics generate net positive feedback on plant growth and the competing plant species do not coexist. When the interaction coefficient is negative ($I_s < 0$), the soil community dynamics generate net negative feedback on plant growth, and, as a result the competing plant species do coexist.

That the dynamics depend upon the sign of the interaction coefficient has two important implications. First, it allows us to identify that the overall pairwise dynamics are not determined by the direct feedback alone. Rather, the pairwise dynamics could be characterized by negative

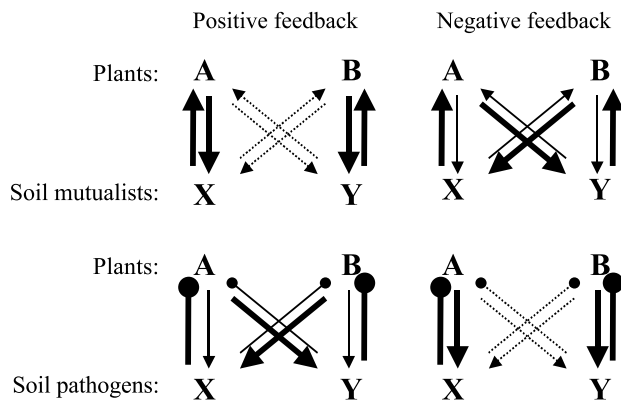


Fig. 2 Depiction of mechanisms of soil community feedback. Here we illustrate fitness relationships that will generate positive and negative feedback on plant growth through changes in the community composition of soil mutualists or pathogens. The arrows and circles indicate the direction of beneficial and detrimental effects, respectively, with the relative strength of these effects being indicated by the thickness of the lines. Positive feedback can result from strongly host-specific soil mutualists and negative feedback can result from strongly host-specific pathogens (as illustrated with the upper left and lower right diagrams). Alternatively, asymmetric fitness relationships within a mutualism could generate negative feedback (upper right figure) and asymmetric fitness relationships between plants and soil pathogens could similarly generate positive feedback (lower right). This latter case could result, for example, if plant A had a high tolerance to pathogen Y (and therefore pathogen Y reaches high abundance with plant A) while pathogen Y has strong negative effects on plant B. As a result, the high initial abundance of plant A results in increased abundance of pathogen Y, which thereafter suppresses plant B.

feedback even if the direct feedbacks were positive (Fig. 2). This point was made explicitly through the development of a variant of the model in the context of interspecific mutualism (Bever, 1999). Similarly, the pairwise dynamics could be characterized by positive feedback even if the direct feedback are negative (Fig. 2). The second implication of this model's result is that the interaction coefficient, I_p , provides a way of testing the importance of the soil community in plant–plant interactions. That is, the growth of two plant species in their own soil communities can be compared to the growth of the two plant species in each others soil communities (i.e. $\alpha_A - \alpha_B - \beta_A + \beta_B$). This is done through home-vs-away contrasts (Bever, 1994; Bever *et al.*, 1997).

Joint effects of soil community feedback and interspecific competition

I extend the previous model (Bever *et al.*, 1997) by explicitly investigating the joint effects of soil community feedback and interspecific competition. I assume linear negative density dependence and competitive effects as has been standard since Lotka and Volterra's path breaking theoretical work. Amending the standard Lotka–Volterra competition model to

include soil community feedback, the rate of increase of plant population A can be written as

$$\frac{dN_A}{dt} = r_A N_A \left(1 + \alpha_A S_A + \beta_A S_B - \frac{N_A + c_B N_B}{K_A} \right), \quad \text{Eqn 1}$$

(N_A , density (or biomass) of plant A; r_A , basal population growth rate of plant A; K_A , carrying capacity for plant A in the absence of soil community feedback and the competition coefficient; c_B , measures the competitive effect of plant B against plant A relative to the density dependent effect of plant A against itself.) The impact of the soil community on plant growth is expressed as a linear function of the composition of the soil community (S_A and S_B), where α_A is the effect of the soil community influenced by plant A on the population growth rate of plant A and β_A is the analogous term expressing the effect of the soil community influenced by plant B on the growth of plant A. The maximum sustainable population size of plant A, \hat{N}_A , is then a function of the soil community composition and the density of plant B, as follows:

$$\hat{N}_A = K_A (1 + \alpha_A S_A + \beta_A S_B) - c_B N_B \quad \text{Eqn 2}$$

Therefore, the maximum sustainable population size would be increased by positive feedback and decreased by negative feedback and is also decreased by depletion of resources by the competing plant species. A symmetric equation for the population growth rate of plant B contains the complementary terms to eqn 1 and can be analyzed similarly.

We reduce the dimensionality of the soil community by assuming that the soil community moves linearly between two extremes, one where $S_A = 1$ and $S_B = 0$ and a second where $S_A = 0$ and $S_B = 1$. Therefore, $S_A + S_B = 1$. This allows the soil community dynamics to be described by a single equation (as was derived in (Bever *et al.*, 1997)) as follows:

$$\frac{dS_A}{dt} = S_A(1 - S_A) \left(\frac{N_A}{N_A + N_B} - v \frac{N_B}{N_A + N_B} \right), \quad \text{Eqn 3}$$

(v , measures the influence of plant B on the soil community relative to that of plant A (Fig. 1).) The soil community does not change when $N_A = vN_B$.

We analyze the dynamics by evaluating the conditions for a plant species to invade a community dominated by a competitor. Invasibility depends upon the soil community composition. As the soil community will be most influenced by the dominant plant, we are particularly interested in the potential of plant A to invade a plant community and soil community comprised of plant B and the soil community influenced by plant B (i.e. $N_A = 0$, $N_B = K_B$, $S_A = 0$), and the ability of plant B to invade a community comprised of plant A and the soil community influenced by plant A (i.e. $N_A = K_A$, $N_B = 0$,

$S_A = 1$). From this we find that either competitor can increase when rare provided that

$$K_A(1 + \alpha_A) < \frac{K_B}{c_A}(1 + \alpha_B) \text{ and } K_B(1 + \beta_B) < \frac{K_A}{c_B}(1 + \beta_A). \quad \text{Eqn 4}$$

These conditions, then, are necessary for competing plant species to coexist. It is consistent with the results from the previous model of feedback (Bever *et al.*, 1997), since under the assumption of equivalent density dependence and competitive equality (i.e. $K_A = K_B$ and $c_A = c_B = 1$) then the conditions for increase when rare (eqn 4) reduce to $\alpha_A < \alpha_B$ and $\beta_A < \beta_B$, satisfying the necessary condition for coexistence as previously identified (i.e. $I_s < 0$). The necessary conditions for competing species to increase when rare (eqn 4) can be reduced to a single condition describing the interdependence on the competitive effects and feedback terms as follows:

$$c_A c_B < \frac{(1 + \alpha_B)(1 + \beta_A)}{(1 + \alpha_A)(1 + \beta_B)} \quad \text{Eqn 5}$$

In the absence of soil community feedback ($\alpha_A = \alpha_B = \beta_A = \beta_B$), a necessary condition for competing species to coexist is that competition between individuals of the same species exceeds competition between individuals of different species (i.e. $c_A \times c_B < 1$). However, with negative soil community feedback, rare species may establish even in the face of strong interspecific competition (Fig. 3).

Thus, the net dynamics in the plant community are codependent on the soil community feedback and interspecific competition. More specifically, negative soil community feedback can drive plant species coexistence under competitive conditions that are not conducive to coexistence as illustrated in Fig. 4. Soil community dynamics, then, can alleviate the restrictive conditions for the coexistence of competitors. Alternatively, there are other conditions in which the two plant species would coexist in the absence of feedback, but do not coexist in the face of strong positive soil community feedback (Fig. 3).

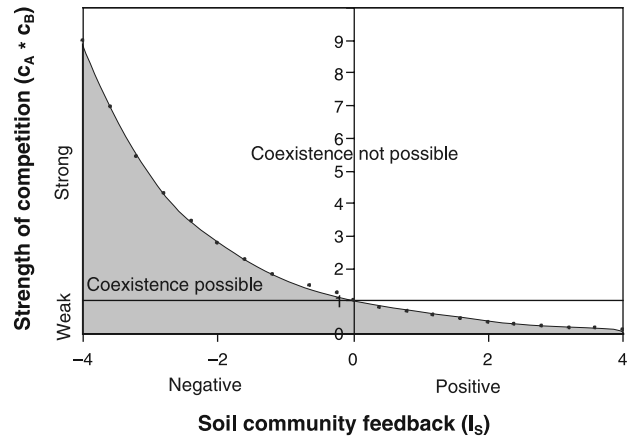


Fig. 3 Conditions for coexistence of competing plant species in the presence of soil community feedback. The shaded region represents the parameter values in which the coexistence of competing plant species is possible as a function of both the strength of interspecific competition and the strength of soil community feedback. The strength of interspecific competition is represented by the product of the competition coefficients ($c_A * c_B$). The strength of soil community feedback is represented by the parameter I_s , where $I_s = \alpha_A - \alpha_B - \beta_A + \beta_B$. In the absence of soil community feedback (i.e. where $I_s = 0$), coexistence is only possible when interspecific competition is weak (i.e. $c_A * c_B < 1$). However, negative soil community feedback increases the possibilities that competing species can coexist. Note that this relationship was calculated assuming that direct and indirect feedback were of equivalent magnitude; the function would vary slightly with differences in the relative magnitude of direct and indirect feedback.

Spatial considerations

The model assumes a well-mixed community (i.e. high dispersal of plants and microbes) and that plant–microbe interactions occur over a large spatial scale. In fact, plants and soil microbes interact on a very local scale (the scale of the plant root system) and plants and soil microbes often have limited dispersal. As a result, plant–soil community interactions occur within a highly spatially structured context. Much work has demonstrated that theoretical expectations

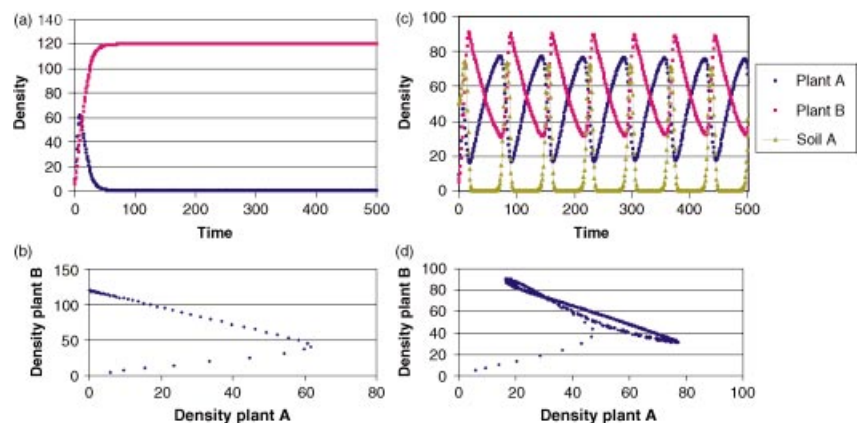


Fig. 4 Illustration of the potential role of soil community dynamics in plant species coexistence. In all simulations, $K_A = 100$, $K_B = 120$, $r_A = 0.7$, $r_B = 0.5$, $c_A = 0.885$ and $c_B = 0.98$. In the absence of soil community dynamics Plant B is a superior competitor and quickly replaces Plant A (a,b). However, the plant species coexist over the long-term in the presence of strong negative soil community feedback ($\alpha_A = -0.03$, $\alpha_B = 0.1$, $\beta_A = 0.1$, $\beta_B = -0.2$, $v = 0.8$). The soil community dynamics drives oscillations in the abundance of the two plant species (c,d).

for well-mixed systems may not hold for systems with high amounts of spatial structure. Spatially explicit models that most directly relate to soil community feedback have been developed as tests of the effect of spatial scale of interaction and dispersal on dynamics due to frequency dependence (Molofsky *et al.*, 2001; Molofsky *et al.*, 2002). Negative and positive soil community feedback will generate negative and positive frequency dependence, respectively. Spatially explicit models indicate that the spatial scale of dispersal and interaction can have strong effects on the spatial structure expected under negative frequency dependence, but spatial scale does not alter the expectation that negative feedback can maintain diversity in a community (Molofsky *et al.*, 2002). This level of spatial structure may also dampen the oscillations generated by the negative feedback, as has been found in predator-prey systems (Caswell, 1978).

The spatial scale of dispersal and interaction has been shown to alter the expected outcome of interactions under positive feedback (Bever *et al.*, 1997; Molofsky *et al.*, 2001). When soil community feedback and dispersal occur over local scales, positive feedback will quickly generate monomorphic clumps, as predicted by the single population models. Local scale positive feedback will then slow the movement of the borders of the clumps and thereby contribute to the maintenance of diversity within separate clumps across a region. Through this mechanism, local scale positive feedback can maintain diversity longer than expected by the random process of drift (Molofsky *et al.*, 2001; Molofsky & Bever, 2002).

Evidence for soil community feedback

Positive feedback

Positive feedback is known to play an important role in plant-soil community interactions. Positive feedback dynamics are evident in the limited success of establishment of plants in the absence of their particular symbionts. This process is dramatically illustrated with the history of establishment of pine forests in the tropics. Attempts at growing pine in Costa Rica failed until trees were inoculated with compatible ectomycorrhizal fungi. With the establishment of their symbionts, pines have very successfully established and are increasingly perceived as a potentially invasive species (Rejmanek & Richardson, 1996). Similarly, the success of plants that are dependent upon AM fungi or N-fixing bacteria are dependent upon the initial abundance of their symbionts (Medve, 1984; Larson & Siemann, 1998). Clearly, positive feedback on plant growth through the soil community can play an important role in plant communities, and these dynamics are likely to contribute to community conversion, and perhaps to the dominance of exotic plant species (Klironomos, 2002). Positive feedback, however, is unlikely to contribute to the coexistence of competitors at local scale.

Negative feedback

There is accumulating evidence of negative feedback playing an important role in structuring plant communities. In agricultural settings, the accumulation of species-specific soil pathogens is known to drive the rotation of crops. For example, the corn-soybean rotation that dominates the landscape of much of North America is driven by the alternating accumulation of species-specific corn and soybean root-feeding nematodes (Agrios, 1997). Work in agricultural contexts has also illustrated that the accumulation of negative soil community feedback may not be a linear process, as repeated cropping of the same crop, while initially resulting in heavy loss of yields, may ultimately generate a soil community that inhibits the host-specific pathogen, thereby reducing the negative feedback (Larkin *et al.*, 1993).

Much of the evidence for the importance of negative feedback in unmanaged communities has come from efforts to test the Janzen-Connell hypothesis that the high diversity of trees in tropical forests results from negative density-dependent mortality (Janzen, 1970; Connell, 1971). Consistent with this hypothesis, seedling mortality in tropical forests has been repeatedly found to increase with the density of conspecifics (Wills *et al.*, 1997; Harms *et al.*, 2000) and with proximity to mature conspecifics (Condit *et al.*, 1994; Webb & Peart, 1999). While Janzen and Connell were originally thinking of species-specific seed predation and insect herbivory as the mechanism for these density and proximity effects, current evidence suggests that accumulation of soil-borne pathogens can be a causal mechanism (Augsburger & Kelley, 1984; Augsburger, 1988). In temperate forests of Eastern North America, the high mortality of wild cherry (*Prunus serotina*) seedlings near adult conspecifics and at high seedling densities have been shown to result from accumulation of soil pathogens in the genus *Pythium* (Packer & Clay, 2000).

There is also accumulating evidence of negative soil community feedback playing an important role in grassland communities. In a series of glasshouse assays of soil community feedback within an old field community in North Carolina, USA, negative feedback was found in nine of the 14 pairwise comparisons tested (Bever, 1994; Bever *et al.*, 1997). In this system, several complementary microbial mechanisms of negative feedback have been demonstrated, including the accumulation of host-specific *Pythium* spp. (Mills & Bever, 1998; Westover & Bever, 2001), host-specific shifts in the composition of rhizosphere bacteria (Westover & Bever, 2001), and host-specific changes in the composition of the AM fungal community (Bever, 2002a,b). The complementarities of the microbial mechanisms of negative feedback may be a key aspect of the consistencies of negative feedback in this system. In an old field in Canada, Klironomos (2002) also found a predominance of negative feedback through the soil community, with pathogenic fungi contributing to the negative feedback. Interestingly, Klironomos (2002) found

that the direction and magnitude of feedback was correlated with the relative abundance of plant species.

Negative feedback has also been found to drive plant community dynamics within sand dune communities (Van der Putten *et al.*, 1993). Again, in this system, complementary microbial mechanisms have been identified, with accumulation of root feeding nematodes working synergistically with pathogenic fungi to decrease plant growth (Van der Putten & Troelstra, 1990; Van der Putten *et al.*, 1990), though the effect of nematodes may be ameliorated by AM fungi (Little & Maun, 1996). In these sand dunes, the negative feedback appears to contribute to species replacement during succession rather than long-term coexistence (Van der Putten *et al.*, 1993). Soil communities have also been suggested as a driver of plant community dynamics in tallgrass prairies (Holah & Alexander, 1999) and European grazed grasslands (Olf *et al.*, 2000). Interestingly, in the latter system, the negative soil community feedback has been implicated as a cause of a shifting mosaic of grassland dominants (Olf *et al.*, 2000), a pattern predicted by spatial simulations of this process (Molofsky *et al.*, 2002).

Directions of future research

Soil community dynamics can theoretically modify the equilibrium population size and contribute to the coexistence or exclusion of competing plant species. Specifically, negative soil community feedback can contribute to the coexistence of strong competitors and so help resolve the problem of the coexistence of plant species that compete for the same soil and light resources. There is growing empirical evidence that soil community feedback is commonly negative and can be strongly negative. A diversity of microbial mechanisms can generate this negative feedback including accumulation of host-specific root feeding nematodes and pathogenic fungi as well as host-specific changes in rhizosphere bacteria and mycorrhizal fungi. In fact, there is evidence of complementarities or redundancies of microbial mechanisms of negative feedback between the same plant species (Westover & Bever, 2001). Such redundancies may explain the consistencies of observation of negative feedback in well-studied systems, as it would reduce the dependencies on initial microbial composition. Together the conceptual and empirical results support the possibility that soil community dynamics may play a key role in plant dynamics and plant species coexistence.

There remain, however, numerous important gaps in our conceptual and empirical understanding of soil community feedback. The approaches taken to testing feedback across studies has been inconsistent, which can limit inferences and generalizations. The theory developed here and elsewhere (Bever *et al.*, 1997) emphasize evaluation of the relative growth of plant species in their own compared to each other's soil communities. Simply testing for decreased growth when

grown with soil communities from conspecifics is not a sufficient test of negative feedback, as it is possible that the soil community also decreases growth of competing plant species.

The theory presented here builds on several simplifying assumptions of unknown influence. For example, the model assumes linear density dependence and linear competitive effects, while density dependence in plants is frequently nonlinear (Watkinson, 1980). Also, as discussed above, plants are also known to interact with soil organisms, and to compete, at a local scale which can modify the competitive outcome. I have also assumed that the rate of change in the soil community feedback are linear with plant density, while there is evidence of nonlinear feedback as a result of both soil trophic interactions and microbial interspecific interference from agricultural systems (Larkin *et al.*, 1993; Neeno-Eckwall *et al.*, 2001). We do not yet know whether nonlinearities are important in less-managed plant communities, though there is clear evidence of microbial interference (Newsham *et al.*, 1995). The impact of such nonlinearities on the role of soil community feedback in plant–plant interactions is also unknown.

There are no empirical demonstrations that negative feedback can permit coexistence of plant species that would otherwise competitively exclude each other. In fact, there are currently only two studies of the joint effects of soil community feedback and interspecific competition to date (Bever, 1994; Van der Putten & Peters, 1997). However, given the evidence that the presence of microbes is known to alter the outcome of competition between plant species (Fitter, 1977; Allen & Allen, 1990; Van der Putten & Peters, 1997; Van der Heijden *et al.*, 1998), we might expect to find that soil feedback could be of similar importance. At a conceptual level, it may prove useful to develop mechanistic models of competition that include soil microbial dynamics and soil feedback (Van der Heijden, 2002).

Much of the empirical focus on soil community feedback in unmanaged systems has emerged only over the last decade. With this short history, there remain many questions as to the direction, strength and mechanisms of soil feedback across a range of ecosystems. At a more general level, we need greater information on how commonly and over what spatial scales do both positive and negative feedback operate simultaneously in a plant community and what are the implications of these interactions. Addressing these empirical and conceptual questions will move us toward a better understanding of the factors determining plant community dynamics.

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